SEASONAL CHEMICAL CHANGES IN THE ROOTS OF SOME SOUTH AFRICAN HIGHVELD GRASSES.

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INTRODUCTION.

Whilst in the past much work has been done in South Africa concerning the investigation of the chemical composition of herbage, particularly with regard to seasonal changes and in relation to fertilizer treatment and grazing intensity, little attention has been focussed on the chemical composition of the roots of grasses and their physiological responses. The results of more recent work, carried out by investigators in various countries, indicate that in many—if not all—perennial herbaceous plants the roots and other sub-aerial parts function as organs of storage. A review of literature relative to this matter has recently been given by the writer (Weinmann, 1940). From the results of all these investigations it appears that particularly during the time of maturation, i.e. after flowering and during seed formation, organic substances as well as mineral elements are translocated from the aerial parts to the underground systems, where they are stored over winter to be drawn upon in the following season for the production of new shoots.

The present contribution reports the results of an investigation into the seasonal chemical changes in the roots of three typical South African Highveld grasses, viz. *Trachypogon plumosus*, *Tristachya hispida* and *Digitaria tricholaenoides*, under varying nutritional conditions. The plant material was collected from camps at Frankenwald, the Botanical Research Station of the University of the Witwatersrand, near Johannesburg.

MATERIALS AND METHODS.

I. General Experimental Conditions.

The camps from which the samples were taken belong to a series of two-morgen camps forming a fertilizer experiment on natural Highveld—known as the "A-camps." The experiment has been described in

detail by Hall, Meredith and Murray (1937). For the present work three camps receiving different fertilizer treatments were selected as localities for sampling, namely :—

(1) the O-camp, receiving no fertilizer treatment,
(2) the PNK-camp, receiving a fertilizer treatment of phosphate, potash and one quantity of nitrogen, and
(3) the PN_3K-camp, receiving the same quantities of phosphate and potash as the PNK-camp, but three quantities of nitrogen.

The quantities of fertilizer applied are per morgen :—

P = 400 lbs. of a mixture of equal quantities of super- and rawrock-phosphate (24% P_2O_5) ;
K = 80 lbs. of muriate of potash (60% K_2O) ;
N = 200 lbs. of sulphate of ammonia (21·1% N) :
N_3 = 600 lbs. of sulphate of ammonia.

These fertilizers are applied in the beginning of the growing season, apart from the additional nitrogen application in PN_3K, which is given in two further equal dressings of 200 lbs. of sulphate of ammonia at convenient intervals during the season. With some insignificant exceptions these treatments have been supplied annually since 1933, when the experiment was established. No phosphate or potash but the usual dressings of nitrogen were given in the season 1936-37.

The camps were grazed in a normal way in rotation during each growing season, but no grazing was done during the season 1935-36, which interval was used to take one series of root samples (below referred to as series I). At the end of this resting period, i.e. during May, the camps were mown.

The fertilized camps (particularly the PN_3K-camp) had been more heavily grazed than the control camp in the preceding years and Glover (1937), who carried out an investigation into the botanical composition of these camps, considered that a deterioration in the vegetation and an increase of bare space had taken place in the PN_3K-camp due to overgrazing. The results of Hall, Meredith and Murray (1937), on the other hand, show a distinct increase of the carrying capacity in both fertilized camps and an increase of the herbage yield at least in the PN_3K-camp.

The surface soil of these camps is an acid, grey-brown loamy sand, poor in organic matter and mineral content, on a subsoil of decomposed granite, interspersed with frequent outcrops of quartz and ouklip (iron sesquioxide). Table I gives the results of a soil analysis of the surface soil.

TABLE I.

Physical and Chemical Properties of Surface Soil.

Percentages of oven dry fine soil.			
Sand	79 ·4	Maximum Water Retaining Capacity	35 ·6
Silt	12 ·0	Loss on Ignition	3 ·0
Clay	8 ·6	Nitrogen	0 ·066
Total Colloids	10 ·4	Phosphoric Oxide	0 ·019
		Potash..	0 ·046

For the mechanical analysis the Boyoucos Hydrometer Method was used (Boyoucos, 1930) ; potash and phosphoric oxide were determined in the hot 10 per cent. hydrochloric acid extract and nitrogen by the ordinary Kjeldahl method.

The rainfall during the season 1935-36 amounted to 35 ·64 inches and during 1936-37 to 32 ·65 inches, which must be considered rather heavy, since normally only ± 25 inches of rainfall per season are recorded in this area.

2. METHOD OF SAMPLING.

Series I.—This series of root samples of *Trachypogon plumosus*, *Tristachya hispida* and *Digitaria tricholaenoides* was taken from the three camps on the following dates : 15th September, 1935, 12th February, 1936, 1st April, 1936 and 20th June, 1936.

In order to obtain representative samples, 36 to 48 tussocks of each species were dug out down to a depth of about nine inches in each camp at each sampling date. The individual root samples of one species taken from the same camp at the same sampling date were united so as to form one sample. Since the camps were again grazed in the following season, another series under protected conditions was initiated.

Series II.—For this series, in each of the three camps a plot of approximately 1/20 acre was fenced off which seemed to be more or less representative of the whole area. In these protected plots samples of *Trachypogon plumosus* were taken at approximately monthly intervals between April 1936 and April 1937. Of these samples shoots as well as roots were utilised. Every sample consisted of ten tufts taken at random from all parts of the plot. The digging out of the roots was done in the same way as in Series I, namely down to a depth of nine inches.

3. Analytical Methods.

When the samples were collected, the bulk of the surrounding and adhering soil was shaken off from the roots after which they were air-dried. Later on the shoots were cut off from the roots and these were properly cleaned with a strong jet of tap water. For this purpose the roots were placed on a fine sieve so that the adhering soil but no roots were washed away. The process of washing lasted not longer than half a minute, thus avoiding leaching of constituents from the tissue. Hereafter the roots were again air-dried, finely ground with a mill and the ground material stored in airtight bottles.

The following chemical constituents were determined in these samples : nitrogen, phosphoric oxide, total sugars and starch.

Nitrogen was determined by the ordinary Kjeldahl method. Phosphorus was estimated by Lorenz's method, i.e. as ammonium phosphomolybdate in the nitric acid extract and included inorganic as well as organic phosphorus—the sample having been incinerated with an excess of saturated lime water (Wiessmann, 1926).

Sugars were extracted with 95 per cent. alcohol and the reducing power of the cleared, deleaded and hydrolyzed extract (for details see Weinmann, 1940) was estimated by the Munson and Walker method (Munson and Walker, 1906), followed by the Bertrand method for the estimation of cuprous oxide (Bertrand, 1906). From the amount of copper precipitate the glucose equivalent was found by reference to the tables of Munson and Walker.

The percentage of starch (including dextrin) was found by digesting the residue from the sugar extraction with saliva (as recommended by Loomis and Shull, 1937, p. 143), and treating the filtrate in exactly the same way as the sugar extract. The glucose value was multiplied by 0·9 to obtain starch.

Estimations of the percentage of total hydrolyzable polysaccharides by the method suggested by Bews and Vanderplank (1930) did not give any conclusive results, neither did the results of potassium determinations indicate any typical seasonal changes ; the results are, therefore, not reported here.

Since the roots of many species are so intimately connected and virtually clad with fine soil particles—mainly silica—that it is not possible to separate them quantitatively from the roots by washing, a determination of ash and dry matter content was carried out for each sample and all analytical results (also those referring to the shoots), were expressed as percentages of combustible (ash-free) dry matter.

TABLE II.

Seasonal Changes in the Chemical Composition of Roots, Series I.

(Results expressed as percentages of combustible dry matter.)

Species.	Date.	O.	PNK.	PN_3K.
NITROGEN.				
Trachypogon plumosus ..	15/9/35	0·69	0·68	0·92
	12/2/36	0·58	0·67	0·72
	1/4/36	0·39	0·50	0·53
	20/6/36	0·69	0·78	0·85
Tristachya hispida	15/9/35	0·61	0·61	0·70
	12/2/36	0·42	0·53	0·66
	1/4/36	0·38	0·41	0·45
	20/6/36	0·54	0·58	0·78
Digitaria tricholaenoides ..	15/9/35	0·65	0·66	0·92
	12/2/36	0·47	0·54	0·60
	1/4/36	0·37	0·49	0·66
	20/6/36	0·58	—(1)	1·04
PHOSPHORIC OXIDE.				
Trachypogon plumosus ..	15/9/35	0·139	0·225	0·192
	12/2/36	0·070	0·152	0·134
	1/4/36	0·070	0·154	0·136
	20/6/36	0·136	0·242	0·290
Tristachya hispida	15/9/35	0·129	0·192	0·140
	12/2/36	0·083	0·139	0·112
	1/4/36	0·075	0·141	0·098
	20/6/36	0·114	0·194	0·193
Digitaria tricholaenoides ..	15/9/35	0·124	—	0·208
	12/2/36	0·065	—	0·124
	1/4/36	0·067	—(2)	0·127
	20/6/36	0·114	—	0·201
TOTAL SUGARS.				
Trachypogon plumosus ..	15/9/35	5·17	5·34	5·58
	12/2/36	1·69	1·42	0·94
	1/4/36	2·22	2·24	1·94
	20/6/36	3·77	4·94	5·16
Tristachya hispida	15/9/35	2·01	2·33	2·68
	12/2/36	1·52	2·18	1·56
	1/4/36	1·36	1·30	1·41
	20/6/36	1·85	2·04	2·06
Digitaria tricholaenoides ..	15/9/35	3·36	3·88	3·32
	12/2/36	2·06	1·27	1·53
	1/4/36	2·57	2·67	2·92
	20/6/36	4·29	—(1)	3·41

(1) Sample lost. (2) Not determined due to lack of sufficient material.

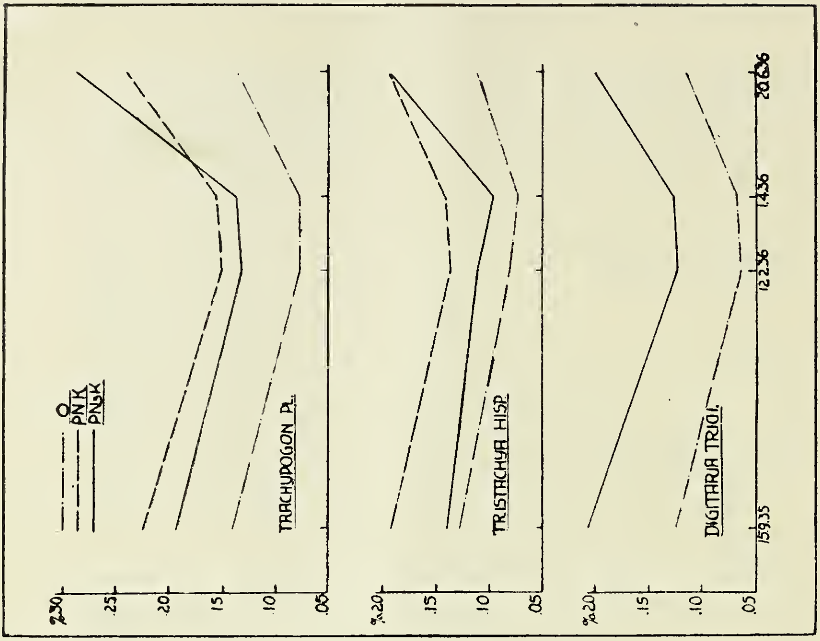

FIG. 2. Seasonal fluctuations of the phosphoric oxide content of roots (Series I).

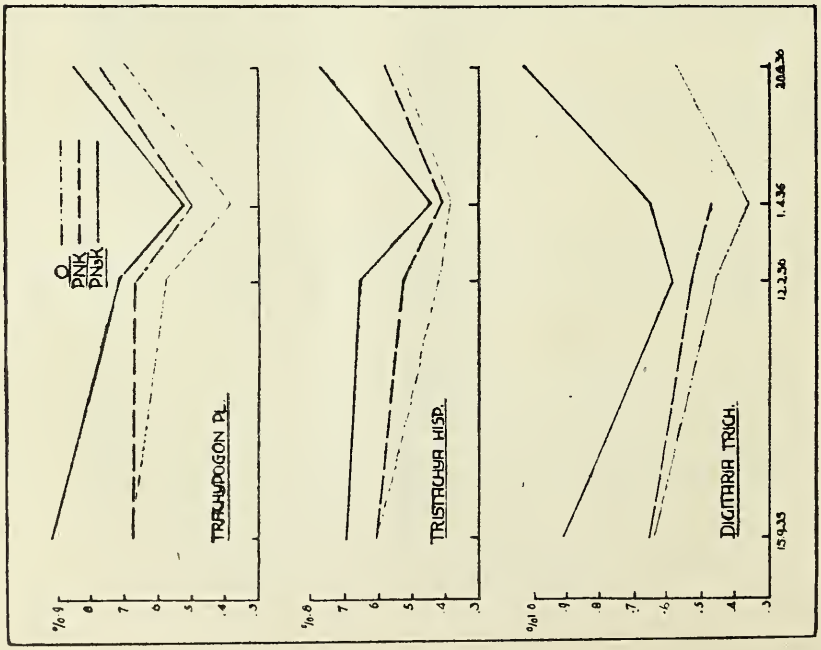

FIG. 1. Seasonal fluctuations of the nitrogen content of roots (Series I).

RESULTS.

Series I.

The percentages of nitrogen, phosphoric oxide and total sugars in the root samples of series I are given in Table II and graphically represented in Diagrams I, II and III.

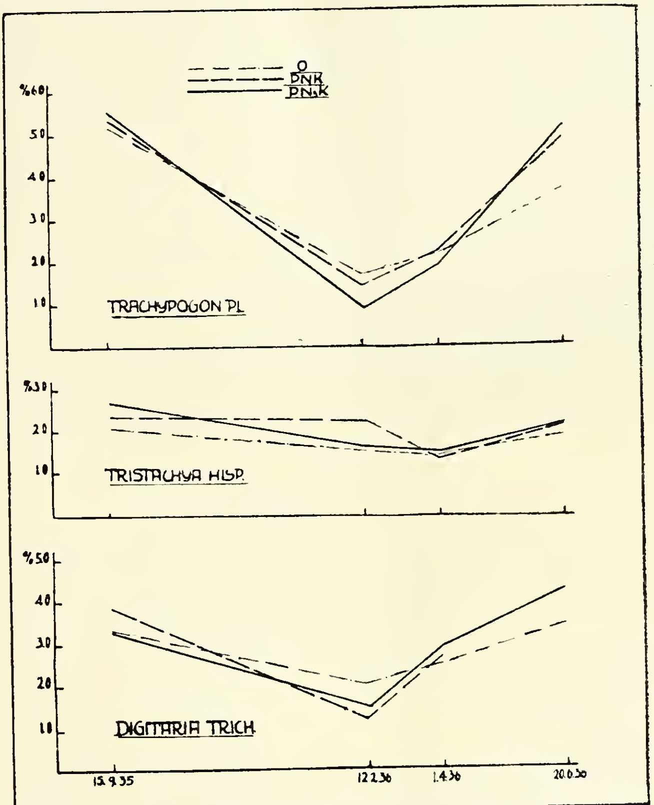

Fig. 3. Seasonal fluctuations of the total sugar content of roots (Series I).

In general, the seasonal curves of these constituents are very similar: in most cases high values are found in winter, i.e. in the September and June samples, and low values in summer, i.e. in the samples taken in

February and April. In all cases there is a distinct decrease in the percentage of these constituents in the first part of the season, followed by an increase in the late part of the season, though the individual curves differ in a number of minor details. Thus, in some cases the minimum value is reached in February, in other cases in April, whilst for phosphorus February and April values are practically the same. The values reached in June in most cases are equal to or at least approach those of the foregoing September. Amongst the sugar curves the seasonal variations are most pronounced in *Trachypogon plumosus* (where the sugar content falls from 5% in winter to 1% in summer and rises to approximately the same level in the following winter), and least pronounced—though still distinct in *Tristachya hispida*, *Digitaria tricholaenoides* being intermediate.

In connection with a study of the growth rhythm of the same three species and also of *Cynodon dactylon*, *Brachiaria serrata* and *Eragrostis chalcantha*, Altona (1939 and 1940), likewise found that the curves of nitrogen and total sugar content in the roots of these grasses in general followed a definite seasonal trend, reaching a maximum in mid-winter and dropping at the time of shooting (spring) to reach a minimum at the time of flowering (i.e. in mid-summer).

Percentage starch was estimated in a selected number of samples: the results are given in Table III.

TABLE III.

Starch Content of Roots, Series I.

(Results expressed as percentages of combustible dry matter.)

	Tristachya hispida.			*Trachypogon pl.*	*Digitaria trich.*
Date.	O	PNK	PN_3K	O	O
12/2/36	4·83	4·52	4·71	0·63	0·42
1/4/36	6·07	7·12	8·05	2·32	0·41
20/6/36	10·87	13·42	13·52	0·34	0·50

The starch content was very low in the roots of *Trachypogon plumosus* and *Digitaria tricholaenoides*, and there was no distinct increase with the advance of the season as it was the case with the percentage of total

sugars. The April value of *Trachypogon plumosus* of 2·32% appears "abnormally" high if compared with the other *Trachypogon* values (see also Table V); it must, however, be regarded as reliable, being the mean of two separate, very closely agreeing determinations (viz. 2·29 and 2·34%). Even so starch cannot be considered to be an important storage material in the roots of these two species. In *Tristachya hispida*, on the other hand, the starch content was very much higher already in summer (4—5%) and increased in all treatments during autumn and winter (up to 11 and 13·5% respectively).

As the figures show, fertilizer treatment did not greatly affect the percentage of total sugars, but increased nitrogen as well as phosphorus content, and in *Tristachya hispida* also the percentage of starch (at least in the April and June samples). PN_3K treatment has in all cases increased the nitrogen content of the roots, if compared with the control, whilst PNK treatment was effective in this direction at least in a number of cases. The phosphorus content was increased by PNK as well as by PN_3K treatment, the maximum values being attained in most cases by PNK treatment.

The differences between the three species are, on the whole, not very consistent, but it appears that in *Tristachya* roots the total sugar content does not reach the same high winter values as in the other two species. On the other hand, as reported above, the roots of *Tristachya hispida* are much richer in starch than those of *Trachypogon plumosus* and *Digitaria tricholaenoides*.

Series II.

The material of this series was used for nitrogen determinations in shoots and roots, whilst phosphorus, total sugars and starch were estimated in a selected number of samples.

Table IV and Diagram IV give the results of the nitrogen determinations in shoots and roots. In the last column of Table IV some phenological observations are recorded which are essential for the full understanding of the data. Table V and Diagram V give the results of the phosphorus, sugar and starch determinations.

The seasonal changes in the chemical composition of the roots agree very closely with those of series I: nitrogen, phosphorus and sugar content increase in autumn, i.e. after flowering, to reach maximal values in mid-winter, and decrease in spring and summer, reaching minimal values in mid-summer. The curves of starch, on the other hand, are different and at the same time less typical. That the lowest starch percentages are found in winter is perhaps due to the extensive accumu-

TABLE IV.

Seasonal Fluctuations of the Nitrogen Content of Trachypogon plumosus, Series II.

(Results expressed as percentages of combustible dry matter.)

Date.	Shoots.			Roots.			Phenological Observations.
	O	PNK	PN_3K	O	PNK	PN_3K	
1/4/36	0·73	0·66	0·65	0·38	0·55	0·56	Plants in full flower.
29/4/36	0·38	0·53	0·49	0·49	0·60	0·59	Still fairly green, seed formation.
30/5/36	0·49	0·46	0·49	0·58	0·67	0·72	Stems yellowish, basal leaves still green, seeds disposed of.
8/7/36	0·31	0·37	0·45	0·74	0·87	0·86	Most shoots dead, few green shoots.
15/8/36	0·38	0·39	0·45	0·67	0·72	0·93	Aerial parts dead.
15/9/36	0·40	0·52	0·53	0·67	0·94	0·98	Old growth partly lost, some new green shoots.
16/10/36	0·55	0·65	0·70	0·64	0·72	0·75	Further loss of old stems.
13/11/36	0·81	0·88	1·17	0·62	0·74	0·79	No more old stems, many young green leaves.
17/12/36	0·84	1·06	1·03	0·47	0·59	0·72	Advanced growth.
15/1/37	0·82	0·84	0·87	0·56	0·72	0·60	Formation of stems.
22/2/37	0·59	0·56	0·70	0·41	0·37	0·49	Begin of flowering.
3/4/37	0·52	0·62	0·55	0·43	0·48	0·53	End of flowering.

TABLE V.

Seasonal Fluctuations of Phosphorus, Sugar and Starch Content of Trachypogon plumosus, Series II.

(Results expressed as percentages of combustible dry matter.)

Date.	Phosphoric Oxide.		Total Sugars.		Starch.	
	Shoots.	Roots.	Roots.		Roots.	
	O	O	PNK	PN_3K	PNK	PN_3K
1/4/36	0·141	0·145	3·69	3·17	0·91	0·49
29/4/36	—	—	—	4·43	—	0·91
30/5/36	0·064	0·164	3·98	—	0·47	—
8/7/36	—	—	5·82	5·30	0·51	1·02
15/8/36	0·049	0·214	4·98	5·05	0·25	0·38
13/11/36	0·149	0·140	3·80	2·13	0·26	0·48
15/1/37	0·136	0·099	1·90	2·08	0·59	0·57
3/4/37	0·095	0·113	2·67	3·05	0·73	0·53

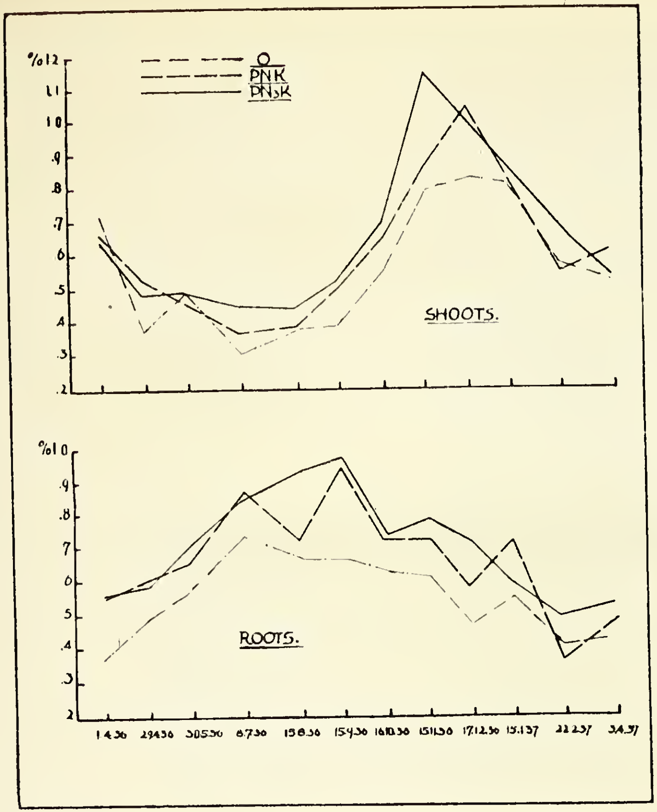

FIG. 4. Seasonal fluctuations of the nitrogen content of *Trachypogon plumosus* (Series II).

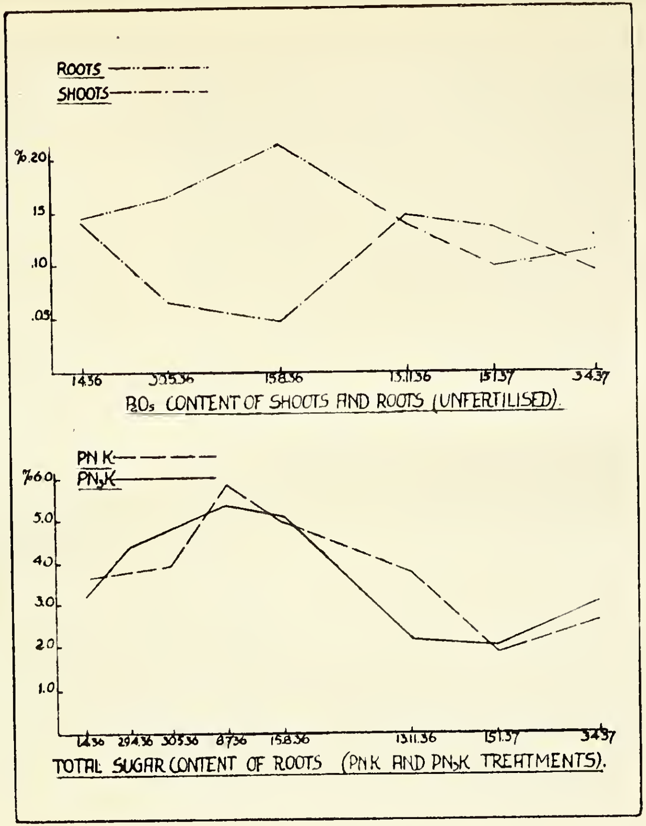

FIG. 5. Seasonal chemical changes in *Trachypogon plumosus* (Series II).

lation of sugars and possibly other materials ; the generally low values of starch, which never appreciably exceed 1%, indicate, however, again that in *Trachypogon* roots not starch but sugars are important as storage materials, the latter reaching values between 5 and 6%.

The chemical changes in the shoots are practically the converse of those in the roots : nitrogen as well as phosphorus decrease in percentage during autumn, reach the lowest point in mid-winter, and rise again in spring, with maxima in November or December ; after this time a rapid decrease occurs. The increase of nitrogen and phosphorus in the shoots after mid-winter is due to new growth, but also to the simultaneous loss of old stems and leaves through wind breakage. If this old growth had been removed, say, in mid-winter, the maximal values would have occurred in early spring, since young leaves are always richest in nitrogen and mineral elements.

Fertilizer treatment has also in this series in general increased the nitrogen content of shoots and roots, though the differences are more significant in the roots.

CONCLUSIONS.

A decrease of the percentages of nitrogen and mineral elements in the herbage with the advancing season has been reported by a large number of workers, in South Africa by Taylor (1922 and 1931), Theiler and associates (1924), Staples and Taylor (1929), Bews and Bayer (1931), Henrici (1932 and 1935) and Hall, Meredith and Murray (1937). When the total amounts of nitrogen and mineral elements present in the shoots of one plant or in the herbage per unit area are calculated, it is shown that absorption actually continues over the greater part of the season. The decrease of the percentages of nitrogen and mineral elements during this part of the season is merely due to the fact that growth and accumulation of carbohydrates proceed at a faster rate than absorption. Calculations carried out by the writer (Weinmann, 1938) have, however, shown that actual losses of total amounts of these substances do occur at the end of the growing season, that is at the time when the percentages of the same substances begin to increase in the roots. Moreover, when grasses, grown in pots under controlled conditions and harvested at different stages of maturity, are analysed, the amounts of carbohydrates, nitrogen and mineral elements lost from the shoots during maturation, are largely recovered in the roots (Richardson, Trumble and Shapter, 1932 and Weinmann, 1940).

All these facts indicate that the seasonal changes in the chemical

composition of roots, as here reported, are mainly due to translocation and storage. Like in many other herbaceous plants, spring growth in these grasses is associated with the translocation of organic reserves and mineral elements from the roots to the shoots, whilst towards the end of the growing season, more particularly after flowering and during maturation, organic reserves elaborated in excess and mineral elements, which are not required any more for functional purposes in the shoots, are translocated from the shoots to the roots where they are stored during winter.

SUMMARY.

Root samples of *Trachypogon plumosus*, *Tristachya hispida* and *Digitaria tricholaenoides*, collected at different times of the season from three camps receiving different fertilizer treatment, were chemically analysed.

Nitrogen, phosphorus and total sugars decreased in percentage in the roots of all three species in spring and early summer, and increased in autumn, reaching a maximum in mid-winter.

Starch was present only in small quantities in the roots of *Trachypogon plumosus* and *Digitaria tricholaenoides*; but occurred in larger amounts in the roots of *Tristachya hispida*, where its percentage likewise increased in autumn and winter, reaching highest values in the roots from well fertilized camps.

Fertilizer treatment also increased the nitrogen and phosphorus content of the roots, but did not appreciably affect their sugar content.

The conclusion is drawn that the seasonal chemical changes observed are mainly due to translocation from shoots to roots and *vice versa* : organic reserves and mineral elements are translocated in autumn and winter from the shoots to the roots, where they are stored, to be drawn upon in the following spring for the production of new top growth.

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